

Quick guide

Archerfish

Stefan Schuster

What are archerfish? Members of a family of seven species of perciform fish, all of the genus *Toxotes*. These opportunistic hunters successfully cope with widely varying environmental conditions and are broadly distributed in mangrove-lined estuaries and freshwater streams of southeast Asia, eastwards from Sri Lanka to Vanuatu (the former New Hebrides) and southwards from the Philippines to Northern Australia.

What is special about these fish? Archerfish have one of nature's most remarkable hunting techniques: they down aerial prey — flies, spiders or even small lizards — from overhanging vegetation with precisely aimed shots of water (Figure 1). A blastpipe formed between a slot in the roof of the fish's mouth and the odd-shaped tongue delivers a shot, the power of which readily dislodges prey at distances over more than ten times the fish's own length. It is amazing how many outstanding abilities come packaged with this peculiar hunting behavior: archerfish spot stationary camouflaged prey; learn to estimate the distance and absolute size of their aerial prey from strongly viewpoint-dependent distorted underwater views; accurately judge three-dimensional target speed; learn to aim their shot from apparently any viewing angle; and form and direct a water stream that is able to hit and dislodge prey with the momentum appropriate for their prey's size.

And in their predictive starts, which they perform in the 100 milliseconds after landing a successful shot, archerfish solve tough problems at an impressive speed. During this critical time, the fish must make sure it is first at the later point of catch, faster than its peers and before

the lateral line mechanosensors of other, competing surface feeding fish are alarmed by the splash. Archerfish attempt this by assessing the initial values of motion of their dislodged prey — the variables, such as initial speed, direction and height that mathematically fix the point of impact. From this, they predict where their prey is expected to land, accurately turn through whatever angle is required and head straight to the later point of catch with a speed matched to its predicted distance so as to guarantee optimal arrival with minimized frictional losses on the way. And all this at a time when their prey has just picked up horizontal momentum — fish fire from positions not directly below the target — and has started its ballistic path.

What do hunting archerfish need to learn? Hardwired neuronal machinery is not the key to the speed and efficiency of archerfish hunting. Even when picking a target the fish are not bound to rigid prey schemes: fish that are used to picking flies will ignore these when firing at them ceases to be rewarding — for instance because a mischievous experimenter glued them to their substrate — and readily switch to any odd-shaped artificial object as long as this regularly yields food when fired at. Also the fish's blastpipe can do more than deliver a simple all-or-none shot: archerfish save energy by tuning their shot to the adhesive forces their prey can maximally sustain. They achieve this in a very simple manner, exploiting what material scientists have only recently discovered: because the maximum adhesive forces of all prey organisms tend to scale universally with size, all the fish needs to know to gauge its shots is prey size. While the gauging of force to size has been evolutionarily matched and inbuilt, recognizing the absolute size of prey isn't and must first be learned.

Learning is also needed to become an accomplished sharpshooter: small fish, of about two centimeters length,

fire charmingly weak shots and improve their range and accuracy by continuous training. But even accomplished sharpshooters that never miss a stationary target are always ready to learn, for instance when challenged with rapidly moving targets which they first are unable to hit. They can eventually meet this challenge by learning to account for the distance the target travelled during the rise time of their shot. Also the archerfish predictive starts involve learning and continuing plasticity. The initial values of prey motion vary over enormous ranges, are not determined *a priori* by the shot and can be combined in every possible way. This makes the task demanding, because the fish must learn to accurately judge the point of impact for all possible combinations of target speed, direction and height. But even solving this by extracting a law that connects the initial values to the point of impact doesn't put an end to further learning. For example, a law learned for small prey items doesn't help to predict the point of catch for large prey whose falling motion is strongly influenced by air friction.

Anything special about the ways in which the fish learn?

The fish appear to learn in ways that most high-school students and perhaps even more their teachers would dream of. A remarkable capability to generalize allows them to readily engage demanding tasks they have not directly been exposed to before. For instance, when the fish learn the size of a rewarding target, they do not do it by storing templates of how the retinal image of an aerial target should look from a given viewpoint; rather, they represent the way in which the retinal image is related to their horizontal and vertical distance from the target and thus can immediately recognize their target from novel views which they haven't encountered before.

A recent finding points to remarkable capabilities

of social learning that fully exploit the fish's capabilities to generalize: bystanders, which initially could hit only stationary targets, acquired the ability to hit rapidly moving targets just by watching a performing team member over an extended period of time without practising a single shot themselves! This remarkable instance of observational learning implies that the bystanders can change their 'viewpoint' and transfer the observed shooting of the performing fish to angles and distances they must later use themselves in order to hit.

What can we learn from fish that chimps or crows haven't already taught us? By studying complex capabilities in more diverse groups we might eventually learn that complex adapted behaviors which are justifiably labeled as 'cognitive' need not rigidly be linked to particular groups of animals or to particular brain regions that house the underlying neuronal circuitry. Such a broader basis would not only help us define more clearly our own position among intelligent creatures, but would also allow us to make use of the biological diversity and to practically profit from what various species have on offer for attacking key issues in cognitive neuroscience.

One of the most exciting possibilities that archerfish, for instance, bring to the field is that they can help us understand how defined small circuits of a few identified neurons perform during a complex sensorimotor task and how they are flexibly tuned to do so. New work suggests that the archerfish predictive start recruits a network of three paired large-field integrating identified reticulospinal neurons that can be monitored *in vivo* with a great wealth of techniques. So, in their predictive starts, archerfish show non-trivial performance with several interesting cognitive components but linked to a network of a few individually recognizable decision-making neurons whose actions we can monitor at



Figure 1. An archerfish in action. (Photo: V. Runkel, S. Schuster.)

cellular resolution. That is not too often the case in vertebrate cognitive neuroscience, and it will be exciting to see how far this will lead us. For instance, comparing the performance of the decision-making neurons in fish that had been trained to different laws of falling motion might give us a clue about the ways in which the animals had 'internalized' these laws and how they fed them into their performing circuitry.

Any practical problems that archerfish can help us solve? You bet! It starts right at the hydrodynamics of shooting: Keeping a water jet from diverging and achieving a focused water mass at the time of impact touches questions of immediate commercial use, for instance in the design of inkjet printers. But their major impact could be that these fish can teach us how to apply fast open-loop strategies to solve complex tasks in robotics. Continuous sensorimotor feedback is computationally costly and takes enormous time even for the fastest computers available today. Therefore, learning strategies that allow restricting the moments of extracting sensory information and getting as far as possible with efficient

'open-loop' strategies could help us speeding up autonomous robots. Archerfish perform various extremely fast open-loop responses on the basis of sensory information taken and processed within impressively short intervals. They can teach us how to design the underlying hardware and how to make it stay tuned to the changing demands of the outer world. Stay tuned.

Where can I find more about archerfish?

- Dill, L.M. (1977). Refraction and the spitting behavior of the archerfish (*Toxotes jaculator*). *Behav. Ecol. Sociobiol.* 2, 169–184.
- Schlegel, T., Schmid C.J. and Schuster, S. (2006). Archerfish shots are evolutionarily matched to prey adhesion. *Curr. Biol.* 16, R836–R837.
- Schuster, S., Rossel, S., Schmidtman, A., Jäger, I. and Poralla, J. (2004). Archer fish learn to compensate for complex optical distortions to determine the absolute size of their aerial prey. *Curr. Biol.* 14, 1565–1568.
- Schuster, S., Wöhl, S., Griebisch, M. and Klostermeier, I. (2006). Animal Cognition: How archer fish learn to down rapidly moving prey. *Curr. Biol.* 16, 378–383.
- Wöhl, S. and Schuster, S. (2007). The predictive start of hunting archer fish: a flexible and precise motor pattern performed with the kinematics of an escape C-start. *J. Exp. Biol.* 210, 311–324.

Universität Erlangen-Nürnberg, Institut für Zoologie II, Staudtstr. 5, D-91058 Erlangen, Germany.
E-mail: sschuste@biologie.uni-erlangen.de